Seaweed diversity patterns in Sub-Saharan Africa

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Abstract

A proper understanding of inshore marine ecosystems cannot be obtained without a thorough knowledge of marine vegetation. This paper summarises our knowledge of species diversity patterns of marine macroalgae in Sub-Saharan Africa, highlighting gaps. In Tropical East Africa the seaweed floras of Somalia and Mozambique are not well known. In Tropical West Africa, only a small number of countries are well-collected, although recent advances, including web-based systems, are ensuring that the information which is available can be more easily accessed. South Africa and Namibia have quite well documented seaweed floras, although detailed collections, especially in the subtidal, or detailed studies of taxa, particularly using molecular methods, anywhere in the region are likely to bring up new records and lead to the discovery of species new to science. South Africa has a very rich seaweed flora (ca. 850 species), due to the presence of species from three of the four major biogeographic regions in sub-Saharan Africa occurring within its borders. Figures for reasonably well-studied countries in Tropical East Africa are more than 400 species, whereas much of Tropical West Africa has lower numbers (e.g. 200 species in well-studied Ghana). Factors which may account for these major differences in seaweed diversity patterns are discussed. Training workshops in Africa are necessary to recruit a body of local scientists able to identify and work with seaweeds, and to make the wealth of information in the international literature available to African marine scientists. A network of national herbaria should contain a collection of correctly identified seaweed species.

Introduction

Seaweeds are particularly useful organisms for studying diversity patterns and planning the conservation and sustainable use of inshore marine resources, and are also useful as indicators of climatic change (see John & Lawson, 1997; Van der Strate et al. 2002; Bolton et al. in press). They are relatively easy to collect, fixed to the substratum, often form relatively stable assemblages, and have relatively similar species numbers in richer temperate and tropical regions. There are four major seaweed floras represented in sub-Saharan Africa. The distinctive but depauperate Tropical West African flora is separated from the species-rich North African temperate flora by a transitional zone extending from about Cap Vert in Senegal to Cap Blanc in Mauritania. South of the equator the West African Flora is very depauperate and only abruptly changes to a temperate flora in northern Namibia (John & Lawson, 1991). The Tropical East Africa flora is more species-rich, and represents only a portion of the much larger flora of the Indo-West Pacific. The latter represents the largest marine biogeographical region on earth, with the greatest diversity of inshore benthic organisms. At the southern tip of the continent are two distinct temperate regions. The west coast of South Africa and the entire coastline of Namibia represent the 'Benguela Marine Province', described as cool-temperate by recent authors (Bolton & Anderson 1997; Stegenga et al. 1997). A distinct and species-rich 'Agulhas Marine Province' is confined to the south coast of South Africa, and has warm temperate affinities.

For the purpose of this review, 'seaweeds' comprise macroscopic marine algae belonging to the Chlorophyta (green algae), Phaeophyta (brown algae) and Rhodophyta (red algae). These phyla are not separated here, although throughout the region around two-thirds of species are red algae, with brown and green algae in relatively similar amounts (although there is a relative increase in green algae going from temperate to tropical South Africa, Bolton et al., in press).

Species diversity patterns will be described in three sections: Tropical East Africa, Tropical West Africa, and South Africa/Namibia. Species numbers are collated on a country basis, as well as on a regional basis within South Africa. The status of our knowledge is summarized, and gaps highlighted.

Tropical East Africa

Documentation

For this review, this comprises the coasts of Somalia, Kenya, Tanzania and Mozambique, with the extreme north of South Africa also having a predominantly tropical flora (see later). The documentation of our knowledge of the seaweeds of this coast received an enormous boost with publication of a comprehensive catalogue of the benthic marine algae of the Indian Ocean (Silva et al 1996, also accessible online http://ucjeps.berkeley.edu/rlmoe/tioc/ioctoc.html). This remarkable document is not entirely tropical in its coverage, since it includes the temperate floras of western Australia and the south coast of South Africa. Reasonable lists of the recorded seaweeds in any country in this enormous region can be extracted. One should, however, always keep in mind that although nomenclaturally and systematically sound (i.e. in each and every case the nomenclaturally correct name of a taxon is used following the most recent systematic opinions at the time of publication), the catalogue is based solely on literature data. Hence, mistakes due to misidentifications are not omitted from the catalogue. This is demonstrated for the brown algal genus *Dictyota*, of which 41 taxa were listed in Silva et al. (1996). In a recent taxonomic revision of the genus by De Clerck (2003) only 23 species are recognized, two of which are new to science and an additional two are reported for the first time for the Indian Ocean. This enormous discrepancy can be attributed to several factors, of which misapplied names resulting from misidentification is the most important one. Other factors include recently proposed synonymies, whereas differing taxonomic opinions are only of minor importance. The problems relating to misapplied names and synonymies are partly related to the enormous size of the Indo-Pacific biogeographical region. As a direct consequence, taxonomists and more floristically-based researchers along the East African coast have to consider research from countries as far as the Hawaiian Archipelago (ca. 15 000 km to the east). Several taxa described from the central Pacific have recently been reported for the western Indian Ocean (e.g. *Dictyota hamifera* Setchell, *Gibsmithia hawaiiensis* Doty, and *Reticulocaulis mucosissimus* Abbott). The vastness of the Indo-Pacific biogeographic region also hampers efforts to produce of a flora covering the East African coast.

A recent bibliometric survey (Erftemijer et al. 2001) analysed a total of 97 publications on seaweeds of the region, that appeared between 1950 and 2000. Tanzania is by far the most important player, whereas several countries contributed not a single publication (Somalia, Reunion, Comores). Applied research made up 43% of all publications (extractable chemical compounds, anti-microbial characteristics, farming, economic potential), whereas 16% was based on experimental work (physiology: particularly from the SAREC Programme Sweden-Tanzania: photosynthesis, pH tolerance, oxidative stress, etc.). A further 19% concerned floristics and distribution of seaweeds, often in relation to exploitation and cultivation, with 8 % taxonomic research and nothing on ecosystem relationships (e.g. nutrient cycling, hydrology, impacts on associated fauna). When broadened to Eastern African marine botanical research as a whole (including mangroves, seagrasses and phytoplankton reseach) the same pattern is evident, with 77% of all research in East Africa being classified as descriptive.

Broader Diversity Patterns

Total seaweed diversity in the region (based on Silva et al. 1996, plus recent additions) is in Table 1.

Table 1.
Seaweed diversity by country in Tropical East Africa

Somalia:	211 species
Kenya:	403 species
Tanzania:	428 species
Mozambique:	243 species

Total for these four countries from Silva et al. (1996) = 678 taxa (species and subspecific taxa).

It is likely that in reality these countries have similar species diversity. Differences in total species number are mainly due to sampling effort. The diversity of Somalia and Mozambique is seriously underestimated (see Bandeira 1998; Carvalho & Bandeira 2003).
As these countries form part of the same large Marine Province, there are great similarities in their marine floras. A comparison of seaweed genera between countries in the Indo-Pacific is presented in Table 1.

Table 2.
Percentage similarities (based on Euclidean distance values) between the seaweed genera in selected countries of the tropical Indian Ocean.

	AUS	INDIA	INDO	KEN	MOZ	SOM	RSA	SRI
AUSTRALIA								
INDIA	83.7							
INDONESIA	83.4	88.2						
KENYA	83.8	88.6	90.1					
MOZAMBIQUE	83.8	87.6	89.2	90.6				
SOMALIA	83.5	87.9	90.1	91.5	90.5			
SOUTH AFRICA	84.0	85.6	85.2	85.5	85.8	84.7		
SRI LANKA	84.1	89.8	90.0	91.5	89.5	90.4	85.7	
TANZANIA	84.0	89.0	89.5	92.8	90.5	91.0	85.4	90.6

Only South Africa and Australia have slightly lower similarity coefficients compared to the other countries included. This difference can be attributed to the significantly lower sea surface temperatures near the southern borders of the Indian Ocean.

The homogeneous sea surface temperature's in the main body of the tropical Indian Ocean, together with a continuous coastline, ensure wide dispersal of marine macroalgae, resulting in a rather homogenous Indian Ocean marine benthic flora.
Flora's become radically different with different temperature regimes. South Africa's east coast (Kwazulu-Natal Province) represents a transition region between a tropical Indian Ocean flora and a warm temperate South Coast flora (Bolton et al., in press, see later). Western Australia represents a similar example.

Detailed Diversity Patterns

The seaweeds of Somalia are poorly studied, and potentially very interesting. On parts of the coast of Somalia and the Southern Arabian Peninsula there is monsoon induced upwelling of cold nutrient rich water, with sea surface temperatures <20°C during the SW monsoon. These cooler water temperatures are reflected in the biogeography of many algae in the Southern Arabian Peninsula (Schils & Coppejans 2003). A common biogeographic pattern includes presence in South Africa, Oman and Australia and absence in the tropical Indian Ocean. Species with this distribution include *Ecklonia radiata, Dictyopteris macrocarpa, Halimeda tuna, Chauviniella spp., Padina boergesenii, Neurymenia nigricans* etc. Although hardly studied, the Somali flora may exhibit the same features.

Studies in these regions, as in most others in Africa, generally are based on collections of larger seaweeds. Many intertidal and subtidal regions are dominated not by these larger seaweeds, but by 'turfs' of smaller species. The latter are ecologically very important, as they may represent a considerable amount of primary production in tropical regions (e.g. Adey & Goertemiller 1987; Larkum et al. 2003 and references therein). A study of these turf communities on the tropical coast of South Africa (Anderson, McKune, Bolton & De Clerck, unpubl.) was carried out by carefully analysing 25 quadrats (25x25cm) at 5 depths at Sodwana. The total sampled area was 1.56 m^2 And 105 species of seaweeds were identified, more than the recorded seaweed floras of many countries in West Africa! (see below).

Tropical West Africa

Documentation

It was only possible to begin to analyse algal diversity patterns in West Africa once all the published data had been critically assessed. This mammoth task began in the 1960's, and the first part of a critical assessment of the seaweeds of tropical West Africa was published by Lawson & Price (1969). Other parts appeared at irregular intervals (Price et al. 1978, 1986, 1988, 1992; John et al. 1979, 1994; Lawson et al. 1995) until the series was completed with publication of the last on the red algal genera (Woelkerling et al. 1998). Underway is a project to update these critical assessments and make the data available early in 2004 as a searchable database on websites at The Natural History Museum, London and the National Herbarium of the Netherlands, Leiden. The searchable database will cover the whole mainland coastline from the northern boundary of Western Sahara southwards to the southern boundary of Namibia, the oceanic islands from Madeira and the Salvage Islands southwards to Ascension and St Helena, and all other islands close to the African mainland coast. The web sites will include a complete bibliography of references to West African algae, compiled by George Lawson.

Lawson and John published, in1982, a book on the coastal environment and marine algae of tropical West Africa with a second edition appearing 5 years later (1987). A more user-friendly identification guide 'The Marine Algae of the Tropical West African Sub-region' is to be published in October 2003 (John et al., 2003). A version was released in 2001 as one of the four reports arising from the project 'Marine Biodiversity Capacity Building in the West African Sub-region', sponsored by the UK Darwin Initiative.

Broader Diversity Patterns

For the purpose of this review, the northernmost limit of sub-Saharan Africa is taken to be Mauritania. The algal floras of the coasts of Mauritania and Senegal are considered transitional between the Temperate West African Flora to the north and the Tropical West African Flora that extends from Gambia southwards to Angola. The diversity of the distinctive West African Flora is significantly lower to the south of the Equator and remains low along the entire length of the Angola coast (Lawson & John, 1991). An abrupt change to a temperate flora takes place in northern Namibia where many cooler water algae are at the northernmost limit of their range. The distribution of the West African Marine Flora bears little relationship to mere latitude but is governed by the movement and cooler water current along the coast. The cooler Canary and Benguela currents run along the western coast of Africa from the north and south respectively thus restricting the occurrence of truly warm-water algae to a relatively narrow band. Even within this narrow tropical band there is local upwelling of cooler and nutrient-rich subsurface water that leads to the surface water falling to as low as 19º C between July and September.

The tropical West African Flora is very impoverished in striking contrast to the richness of the Caribbean region of the eastern Atlantic or the tropical coast of east Africa. Like the western shores of other continents, coral reefs are absent and consequently so is the rich and varied life associated with these structures. As a result of the absence of protecting coral reefs or shallow offshore shoals, much of the West African coast is very wave exposed. Seagrass meadows are not present except in more sheltered parts of the Mauritania coast and the shallow tidal inlets south of Luanda in Angola. Seasonal upwelling, seasonal inflow of turbid, silt-laden water, seasonally lowered inshore salinity, absence of suitable shallow water substrata, low habitat diversity and heterogeneity are all factors contributing to the absence of coral reefs and the low species diversity of algae n tropical West Africa. An especially important cause of the low diversity is likely to be a historical one. There is now much evidence to show that during the Pleistocene glaciations the 20º C winter isotherm moved laterally during winter about 15-20 degrees of latitude towards the Equator thus eliminating the tropical zone. Since that time, the West African region would have become recolonized by species from the tropical eastern Atlantic that remained unaffected during the Pleistocene. The recolonization of tropical West Africa would explain its poverty, low endemism and floristic similarity to the eastern Atlantic.

Detailed Diversity Patterns

The figures for algal species diversity for each of the countries and inshore islands in the West African region (Table 3) are based on the web-site database, prepared by John, Prud'homme van Reine, Lawson, Price and Kostermanns.

Table 3.
Seaweed species diversity for the West Africa Sub-region including the Gulf of Guinea islands as well as St. Helena and Ascension (based on data compiled by John, Prud'homme van Reine, Lawson, Price and Kostermanns).

Western Sahara	81
Mauritania	212
North Sénégal	274
Gambia	62
South Sénégal	33
Guinea-Bissau	12
Guinée	21
Sierra-Leone	112
Liberia	88
Côte d'Ivoire	86
Ghana	200
Togo	37
Benin	16
Nigeria	49
Cameroun	86
Bioko	31
Principe	25
São Tomé	95
Equatorial Guinea	0
Gabon	83
Republic of Congo	18
Cabinda	2
Zaire	9
Angola	117
Namibia	196
Ascension	65

St. Helena	47
Annobon	37

Species totals:

Angola to Gambia (includes Gulf of Guinea islands) = 382 species
Angola to Mauritania = 583 species

Many reasons account for the considerable variation in species diversity within tropical West Africa. One of the more obvious is intensity of collecting. The algal lists for many countries are based on collecting visits of less than one week (often by Lawson and John). One of the coastal regions for which there is no modern data is that of 'Loango', the name used especially by 19th century collectors for what is known as the Republic of Congo, Zaire as well as Cabinda. There are little data for adjacent Gabon and Cameroun with the most recent collecting visits made by Lawson and John who just spent a few days in each country in 1974. Angola has been relatively well covered thanks to a 5 weeks collecting visit by John, Lawson and Price; they surveyed its coast in January and February 1974. In November 1975 Lawson and John spent 5 days collecting algae in both Gambia and Liberia although three years earlier John had spent a day in southern Liberia and several days collecting along the coast of Côte d'Ivoire.

Islands in the Gulf of Guinea have rocky shores and remain undercollected. Lawson spent a week collecting in Bioko, and in the 1950s several collections were made along the coasts of São Tomé and Principe, including during a visit by the research vessel 'Calypso' in 1956. The countries with the highest algal diversities ('hot spots') tend to be those most intensively investigated and these include Sénégal, Ghana and Sierra Leone. There have been almost 40 research publications dealing with the algal of these three countries, whereas the large majority of countries in the region have less than 3 publications mentioning their algae (John & Lawson 1997).
Sampling intensity and the competence of those identifying the material are factors accounting for West African algal diversity patterns (Table 3). There is no doubt that Sénégal, Ghana and Sierra Leone represent 'hot spots' of algal diversity and have often attracted attention only because rocky shores suitable for attached algae are present. There are many other countries where the coast is characterized by long sandy beaches, and extensive mangrove areas fringing deltas, estuaries and lagoons dominate. Not unexpectedly the diversity of algae is low in such countries, and they represent 'cold spots' of algal diversity. Further collecting, however intensive, is unlikely to significantly increase the low numbers of recorded algal species. . The absence of suitable shores probably accounts in large part for the low algal diversity of countries such as Nigeria, Guinea Bissau, Guinée, Togo and Benin. Often the only significant algal development in these countries is on man-made structures (e.g. breakwaters, oil rigs). Subtidal algae are also under-represented with the only SCUBA-diving collecting having taken place in Ghana, Angola and, possibly, during the visit of the 'Calypso' to the Gulf of Guinea islands in 1950's. The importance of subtidal collecting has been demonstrated by John & Lawson. (1997) who found that 60% of the algae collected in Ghana were predominantly intertidal, and the remainder subtidal. This clearly demonstrates the need to SCUBA-dive in order to obtain a meaningful picture of marine algal diversity. Otherwise for many countries the only subtidal records of algae are based specimens cast up on the beach or dredged.

Future Priorities

A future priority is to conduct further basic shore survey work in order to fill the many gaps that exist in our knowledge of marine diversity patterns in tropical West Africa. The focus of future work should be on those countries known to have rocky shores, which have been under-collected in the past. Seasonality has to be taken into account with visits taking place during the 'wet' and 'dry' seasons, as well as during any period of upwelling. SCUBA-diving is crucial, since remote sampling of submarine rocks frequently gives a misleading impression of marine algal diversity.

Of paramount importance is the accurate identification of the algal samples. This is a very real problem in West Africa, despite the availability of a new user-friendly identication guide covering at least part of tropical West Africa (John et al. 2001). In the virtual absence of any indigenous expertise in algal taxonomy there is an urgent need to run training courses. These courses in algal identification should be given by competent algal taxonomists, and based in Africa. All such courses would need to include training in sampling, preservation of material, as well as curation and databasing of specimens, since material collected during shore surveys needs to be deposited in national herbaria for future reference and study. The setting up and/or strengthening national herbaria should be another regional priority.

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Namibia/South Africa

Documentation

Namibia and South Africa can logically be discussed together as 'temperate southern Africa'. The seaweeds of these two countries are becoming increasingly well documented in the last few years. South African west coast seaweeds were documented in detail in Stegenga et al. (1997). Recently there have been two Ph.D. theses on the seaweeds of Namibia (Engeldow 1998; Rull Lluch 1999), the former mostly ecological and biogeographic (e.g. Engeldow & Bolton 2003), and the latter primarily taxonomic. The thesis of Rull Lluch (including some additional information from the thesis of Engledow) has been published recently in English, as a Flora of the seaweeds of Namibia (Rull Lluch 2002). The known seaweed diversity of South Africa has increased from 547 species in 1984 to around 850 today, making it one of the richest regions globally for seaweed species. Detailed studies of the distribution patterns of South African seaweeds are under way (Bolton & Stegenga 2002).

Broader diversity patterns

These two countries can be divided into a number of biogeographical regions, with differing seaweed floras (Bolton & Anderson 1997; Bolton et al. in press). The West Coast (or Benguela Marine Province) includes the entire coast of Namibia, and the west coast of South Africa as far south as the Cape Peninsula. This region is dominated by upwelling of cool water (often around 10ºC) from the Benguela current. The west coast flora is relatively species poor in comparison with other temperate floras, and with the south and east coast floras of South Africa (see Table 4).
Thus Namibia, with almost 200 species recorded, is a fairly rich flora in the context of West Africa, but this is a low number in relation to the rest of southern Africa.

Table 4
Seaweed species numbers in various regions of temperate southern Africa

Namibia (Lluch 2002)	196 spp,
South Africa (total)	850 spp.
South African regions:	
West coast (Orange River to Cape Peninsula)	213 spp.
West coast plus West/South coast overlap (Orange River to Cape Agulhas)	421 spp.
South coast (Cape Agulhas to Port Edward)	471 spp.
East Coast (Port Edward to Kosi Bay)	507 spp.

The known seaweed flora of South Africa has risen from 547 species in 1984, to around 850 today, following a number of detailed collections and taxonomic studies by Richard Norris on the east coast, Stegenga, Bolton & Anderson on the west and south coasts, and a recent collaboration on the east coast between Bolton & Anderson and a group from the University of Ghent, Belgium (Coppejans, De Clerck and colleagues) (Bolton 1999; Bolton et al. 2001). It is now known to be one of the world's richest seaweed floras. The richness of the South African seaweed flora arises from the fact that it inhabits a large section of predominantly rocky coastline where three distinct biogeographical regions overlap.

Both the west and south coast floras have high levels of endemism, with 327 seaweed species present in South Africa being endemic to South Africa and Namibia (38.5% of the South African flora).

Local diversity patterns

The distribution of South Africa seaweeds is being analysed in detailed in a series of 58 x 50 km coastal sections (see Bolton & Stegenga 2002). The number of species present in each coastal section is around 150 on the west coast, but 250-300 species per section on the south and east coasts. This diversity pattern is also shown in Table 4 (calculated from the same data set), with a total of 213 species on the west coast proper, but 471 species on the south coast, and 507 species on the east coast. While percentage endemism is similar at any point on the west and south coasts, most endemic species occur in the richer south coast flora. A 50km coastal section on the south coast can contain up to 300 species of which around 125 species are endemic to temperate southern Africa. The east coast of South Africa (Kwazulu-Natal Province) consists, from the seaweed data, of a gradual overlap between the south coast flora and the tropical East African flora. In a recent study (Bolton et al. in press) is has been shown that the region of most rapid change is in the extreme east of the South African coastline. The flora of the two easternmost 50km coastal sections (containing Sodwana Bay and Kosi Bay) is predominantly tropical. The next section, moving southwest (St. Lucia/ Cape Vidal), has relatively equal numbers of temperate south coast and tropical species. Thus the extreme easternmost portion of the South African coast is considered the limit of the tropical Indian Ocean flora.

Concluding comments

As mentioned in the Introduction, a proper knowledge of seaweed diversity is essential for an understanding of the ecological functioning of inshore marine systems. In addition, seaweeds have both current and potential direct economic benefits. A large coastal industry is based on the aquaculture of *Eucheuma*/*Kappaphycus* (material originally introduced from the Philippines) for carrageenan in Tanzania, more recently Mozambique, and with a pilot project in Kenya. Other significant seaweed industries exist in South Africa and Namibia (*Gracilaria* and *Gelidium* for agar; kelp, *Ecklonia* and *Laminaria,* for alginate, abalone feed, etc.) (Anderson et al. 2003). As well as these traditional industries, there is a large literature on the potential uses of seaweeds, much of it concentrating on a wide array of chemicals which seaweeds produce. For example, of the 357 seaweed genera, which have been recorded in South Africa, no less than 127 (36%) occur in the literature as containing documented bioactive compounds (AJ Smit, unpublished).

A good basis for the study of the seaweeds of Sub-Saharan Africa exists. There is clearly a great need for efforts to make this information available in many of the countries in sub-Saharan Africa. Seaweeds are difficult to identify correctly without a compound microscope, and a body of trained personnel is required in each region for this purpose. While websites are very useful at disseminating information, they seldom include the required information to identify species – many consist of lists, sometimes with a photograph. Funding agencies have not, in the recent past, generally supported the detailed documentation of taxonomic diversity, and because of this the numbers of trained seaweed (or indeed algal) taxonomists in the region are very few.

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